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MORPHOLOGICAL TRAITS AND INVASIVE POTENTIAL OF THE ALIEN *EUPHORBIA TERRACINA* (EUPHORBIACEAE) IN COASTAL SOUTHERN CALIFORNIA

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ABSTRACT

Euphorbia terracina L., also known as terracina spurge, is a Mediterranean Basin perennial that has recently become invasive in southern California and is actively spreading at a virtually exponential rate along coastal areas in Los Angeles County. The National Park Service (NPS) is undertaking measures to treat and control further spread of current populations, but little is known about the plant's ecology and impact on native plant communities. This study reviewed the existing information on *E. terracina* and investigated populations established in Solstice Canyon in coastal Los Angeles County. Populations of *E. terracina* were compared in two different habitats in Solstice Canyon: in an open site along an old road and a shaded riparian site subject to past disturbance. Both open-disturbed and shaded sites had high aboveground biomass densities, with the highest density in the open, disturbed site. Sites differed in biomass allocation and specific leaf area (SLA) between sites, with plants at the open site having significantly lower specific leaf area than those at the shaded site. Open site plants also had high SLA compared to native coastal sage scrub species. *Euphorbia terracina* produces large quantities of seeds that do not show dormancy. Seeds germinated well under low light intensities without mechanical or chemical treatment. *Euphorbia terracina* possesses numerous traits — success in disturbed sites, phenotypic plasticity, high SLA compared to native species, high reproductive output, and seeds lacking dormancy — that have been associated with invasive species and likely contribute to both its success and the difficulty in treatment and control of established populations.

Key Words: biomass allocation, *Euphorbia terracina*, germination, invasive, phenotypic plasticity, specific leaf area.

Euphorbia terracina is an invasive herbaceous perennial from the Mediterranean Basin that has recently established in coastal areas of Los Angeles County in southern California. The plant's prior invasive history and wide distribution in Australia, where *E. terracina* has naturalized to and invaded disturbed areas of nutrient-poor sandy soils in the coastal heath of Victoria, South Australia, and New South Wales (Randall and Brooks 2002), suggest *E. terracina* is likely to be a successful invader elsewhere in the world (Reichard and Hamilton 1997). In southern California, however, *E. terracina* is not restricted to coastal sandy soils and has naturalized to both coastal bluff and sage scrub habitats. Although multiple points of origin are possible, a major center of its spread appears to be the central Malibu coast. *Euphorbia terracina* has since expanded its range west and east along the Malibu coast and up into canyons of the Santa Monica Mountains with remarkable aggressiveness, often forming dense monocultures in disturbed areas. It has been reported along Highway 150 in Ventura County and from coastal areas of the Palos Verdes Peninsula in southern Los Angeles County (P. Rundel, personal observation).

Despite its current abundance in coastal southern California, *E. terracina* is not listed in the Jepson Manual (Hickman 1993) and little is known about the species. The first known collection of *E. terracina* was made at the El Segundo Dunes near the Los Angeles International Airport in 1987 (Hrusa et al. 2002) and the National Park Service (NPS) only became aware of its spread in the late 1990's. The objective of this study is to provide a review of existing literature on current *E. terracina* distribution and to develop a better understanding of the ecology of *E. terracina* to aid in the control and management of populations in coastal southern California. Field and laboratory studies were implemented to investigate the invasive potential of *E. terracina* in southern California.

Previous studies have proposed that morphological plasticity in response to varying environmental conditions enables non-native species to successfully invade a range of habitats (Baker 1974; Schweitzer and Larson 1999; Daehler 2003; Parker et al. 2003). *Euphorbia terracina* plants were compared between two sites with differing disturbance and light conditions in Solstice Canyon, Malibu California: an open-disturbed habitat along roadsides and trails and a riparian woodland habitat. Successfully established plants were expected to differ in biomass allocation and specific leaf area (SLA) between these sites. In addition, reproductive characteristics of *E. terracina* were investigated to better understand the plant's success as an invasive. Invasive species often lack seed dormancy, readily germinating without chemical treatments (Reichard and Hamilton 1997). Thus, *Euphorbia terracina* was expected to require little or no pre-germination treatment for successful germination.

MATERIALS AND METHODS

Species Ecology

Euphorbia terracina, also called terracina spurge, false caper, and Geraldton carnation weed (in Australia), is an herbaceous perennial in the Euphorbiaceae. Its native habitat is dry, sandy soils along the coasts of islands and adjacent mainland of the Mediterranean Basin, extending northwest from the Iberian Peninsula to the eastern Mediterranean in Croatia and Greece (Tutin et al. 1968). Mature plants grow to 1 m and contain a noxious, milky sap common to many *Euphorbia* species. Plants are simple, branched with 0–5 auxiliary shoots arising from the base of the plant, and grow from a root crown with a long taproot (Tutin et al. 1968). The leaves are dark green, minutely serrate, and alternate. Each shoot produces 4 to 5 equal-length pedicels arranged in clusters at the stem apex. *Euphorbia terracina* has small, inconspicuous yellow to green flowers, which are surrounded by five pointed, oval bracts. Each flower produces a small three-lobed fruit with each lobe containing one seed. *Euphorbia terracina* has a great reproductive capacity, as each shoot is capable of producing up to 200 seeds (C. Brigham, personal communication). Seeds are dispersed explosively from fruits, traveling up to 5 m from the plant (C. Brigham, personal communication). Flowering begins in spring and seeds are produced in summer. Although plants may die back with water stress in late summer, new stems surface from the original root crowns at the start of the next growing season (P. Rundel, personal communication). Seeds may germinate in any month of the year and young plants are capable of branching repeatedly to form dense clusters before spring flowering. While *E. terracina* does not reproduce vegetatively, plants cut at their base prior to setting seed rapidly grow new stems using carbohydrates stored in their taproot (P. Rundel, personal communication).

Field Sites

Solstice Canyon in Malibu, California (34°S, 118°W) appears to be a center of introduction of *E. terracina* into coastal southern California and has large *E. terracina* populations. It receives a mean annual rainfall of about 330 mm, with considerable interannual variation. Temperature conditions are mild throughout the year, with mean maximum summer temperatures of about 21°C and mean winter minimum temperatures of about 10°C. Field sites were selected within Solstice Canyon to compare populations of *E. terracina* in an open-disturbed and a shaded riparian woodland habitat. The open site (a 20 × 30 m plot) was located on a gentle, dry slope in full sun, having high disturbance from past mowing and bordering hiking trails. The shaded study site was a 25 m × 5 m plot in a riparian woodland corridor about 400 m west of the open site; it was located 10 m from the creek and approximately 25 m from any trail. (The study plots differed in size because *E. terracina* populations differed in size between sites.) All field data and observations were collected between May 10 and June 23, 2004.

Biomass Allocation Comparisons

Euphorbia terracina aboveground biomass was harvested from ten randomly selected 0.3 × 0.3 m plots at each site. The allocation of *E. terracina* aboveground shoot biomass to reproductive, photosynthetic, and structural tissue was then determined for both sites using five representative plants from each of the 0.30 × 0.30 m samples. These five plant samples were pooled to generate one sample per plot (n = 10). Each shoot was separated into three organ types. All fruits, developed buds, and flowers were classified as reproductive organs; flower bracts and leaves as photosynthetic organs; and remaining stems as structural organs. The number of flowers, developed buds, and fruits were counted for each plant. All plant material was dried at 85°C for 48 hrs prior to weighing. The relative biomass allocation of each organ component per shoot was calculated for open and shade populations. Means for sun and shade sites are reported as mean ±1 standard deviation (SD). Student's t-tests were used to determine if there was a significant difference in the allocation of biomass between plants in the open and shade populations. Student's t-test was also used to compare estimations of total aboveground biomass between sites. The experiment-wide error rate was adjusted using the Bonferroni method to take into account elevated error caused by three comparisons on the biomass data (Gotelli and Ellison 2004). Based on the Bonferroni correction, P-values of 0.01667–0.05 were considered suggestive, rather than significant. All statistics were preformed using SAS Institute, Inc. Statview® (version 5.0) software.

Leaf morphology also was compared between open and shade plants. On May 24, 2004, all leaves from five shoots were randomly harvested from each site (Open site $n = 60$, shade site $n = 64$). The leaf area for both open and shade plants was measured using a LI-COR, Inc. Leaf Area Meter, model LI-3100. The leaves were then oven-dried and weighed to determine their specific leaf area (SLA). A LI-COR Solar Monitor, model LI-1776 was used to measure light intensities at *E. terracina* canopy height and at ground level below the canopy for both sites. Measurements were taken at 14:20 for the open site and 14:40 for the shade site on June 23, 2004. The open site had a light intensity of 1800 ± 190 µmol m^{-2} s^{-1} (mean ±1 SD) at canopy height and 720 ± 340 µmol m^{-2} s^{-1} at ground level. The shade site had lower light intensities of 70 ± 31 µmol m^{-2} s^{-1} at canopy height and 41 ± 17 µmol m^{-2} s^{-1} at ground level.

Germination Experiments

Mature seeds were collected directly from representative plants in the open site to investigate seed germination. Germination experiments were performed within one week of seed collection. Seeds were germinated in the lab under low-light intensity of 2 µmol m^{-2} s^{-1} at a temperature of 24°C. Light intensities were measured using a LI-COR Solar Monitor, model LI-1776. To determine if *E. terracina* seeds possess seed dormancy preventing germination, aside from the mechanical barrier of the seed coat, two seed treatments were prepared; a scarification treatment and a control treatment with no scarification. Seeds were scarified immediately prior to the germination experiments using a fine, sharp needle to puncture a small hole in the seed coat. There were five replicates of 20 seeds each per scarification treatment. Seeds were placed on wet filter paper in 9-cm diameter petri dishes. Moisture in the dishes was maintained constant with de-ionized water. Seeds were recorded as having germinated once the radicle emerged from the seed coat. The number of germinated seeds per replicate was recorded every 24 hr for up to 21 d, or until the number of germinated seeds per treatment remained constant for over 48 hr. Mean percentage germination for each treatment ($n = 5$) were compared using a t-test (SAS Institute Statview® [version 5.0]), and values reported as mean ±1 SD.

RESULTS

While *E. terracina* had high aboveground biomass at both open and shade sites, aboveground biomass was significantly higher at the open site (Fig. 2) ($t = 11.379$, $DF = 98$, $P < 0.001$). The mean sum of structural, photosynthetic, and reproductive biomass was 324.2 ± 71.8 g m^{-2} ($n = 10$) in the open site compared to 118.8 ± 43.1 g m^{-2} ($n = 10$) in the shade site ($t = -0.661$, $DF = 18$, $P < 0.001$) (Fig. 2). The considerable difference in the mean sum of biomass between open and shade sites can be contributed to the large difference in structural biomass between sites (open: 239.8 ± 56.8 g m^{-2} and shade 76.0 ± 35.5 g m^{-2}) (Fig. 2). The difference in biomass of photosynthetic organs between open and shade sites, however, was only suggestive ($t = -2.275$, $P = 0.0362$ (adjusted $\alpha = 0.0167$)). *Euphorbia terracina* also showed differences in the relative biomass allocation to different organs between sites (Fig. 3). Shade site plants had a significantly greater relative photosynthetic tissue biomass than open site plants. Sun plants had significantly higher relative biomass allocation to structural ($t = -5.372$, $DF = 98$, $P < 0.001$) and reproductive ($t = -7.124$, $DF = 98$, $P < 0.001$) tissues than the shade plants because of their taller stature. There was not a significant difference in the number of flowers ($P > 0.05$), but the relative allocation of biomass to reproductive tissues in the sun population was three times higher than that in shade populations. Open site plants also had a significantly lower specific leaf area of 0.192 ± 0.014 cm^2 mg^{-1} compared to shade plants with 0.464 ± 0.046 cm^2 mg^{-1} ($t = 44.193$, $DF = 122$, $P < 0.001$) (Fig. 4, Table 1).

The germination experiments showed that *E. terracina* seeds readily germinate under controlled laboratory conditions. Scarification had no significant effect on final percent seed germination under low-light (2 µmol m^{-2} s^{-1}) laboratory conditions ($t = 1.00$, $DF = 8$, $P > 0.1$). Control treatments had a final germination percentage of $100 \pm 0.00\%$ and scarified treatments have a final germination of $98 \pm 4.47\%$. Scarification did have an effect on the rate of germination, as scarified seeds germinated faster than the control seeds (Fig. 5). The number of days required to reach maximum percentage of germination was 6.6 ± 0.89 d in scarified treatments ($n = 5$) and 12.6 ± 1.52 d in control treatments ($n = 5$).

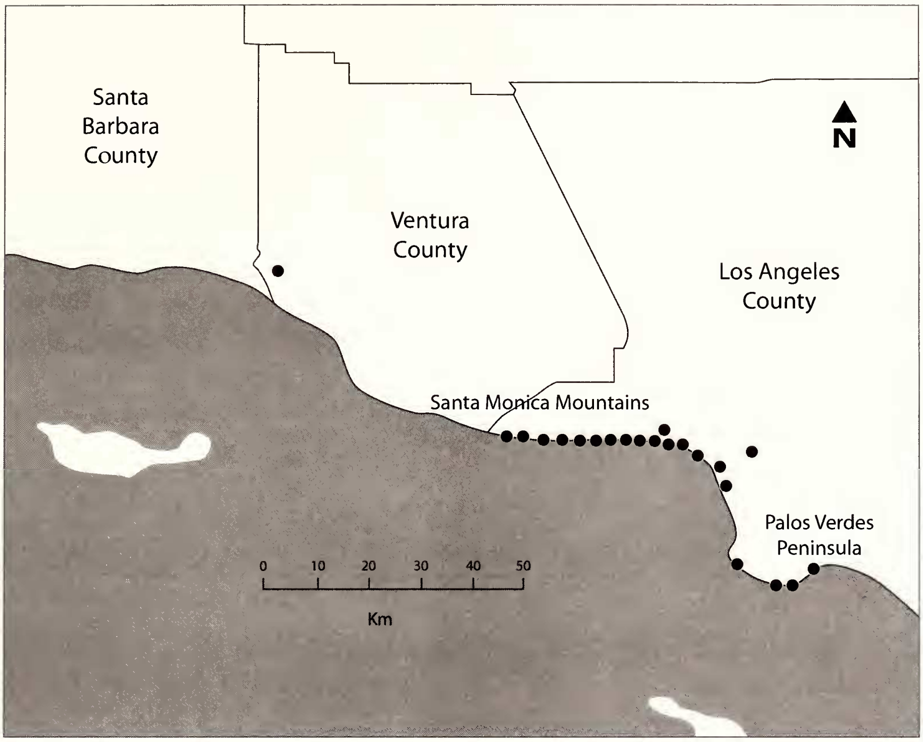

FIG. 1. Distribution of *Euphorbia terracina* in Southern California.

DISCUSSION

In Solstice Canyon, *E. terracina* has become widely and successfully established in both an open, disturbed and a shaded, riparian woodland site, indicating a capacity to invade a range of habitats in southern California. The notably higher *E. terracina* total and reproductive biomass in the open site suggest high light availability and disturbance provide better conditions for *E. terracina* success. Disturbance often promotes the invasion of non-native species that are well adapted to high light environments associated with disturbance (Hobbs and Huenneke 1992; Burke and Grime 1996). Frequent mowing has been employed to control a variety of weed problems at the open site, potentially stimulating *E. terracina* biomass production. Low relative allocation to leaves and high reproductive output, as exhibited in *E. terracina* at the open site, have been interpreted as responses to high light environments (Givinish 1988; Rice and Bazzaz 1989). However, because biomass collection is pseudoreplicated (Hurlbert 1984) between single open and shade sites, the study cannot definitively determine if light availability was responsible for the greater *E. terracina* establishment and success at the open site. For example, a competitive advantage for other resources, such as nutrients or water, compared to native species could also influence *E. terracina* success (Crawley et al. 1999; Callaway and Aschehoug 2000; Baruch et al. 2000).

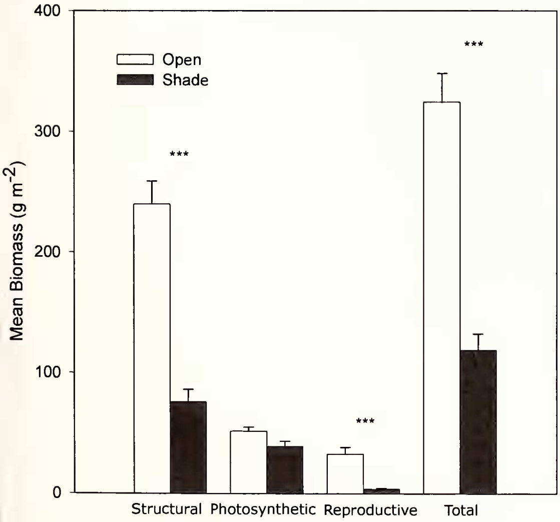

FIG. 2. The mean total, structural (stems), photosynthetic (leaves and bracts), and reproductive (flowers and fruits) biomass per m^2 of *Euphorbia terracina* plotted + 1 standard error for open (n = 10) and shade (n =10) sites. *** Indicates $P < 0.001$ significant difference between open and shade values.

The ability of *E. terracina* to form dense monocultures given optimal high light conditions makes it a considerable threat to native flora in

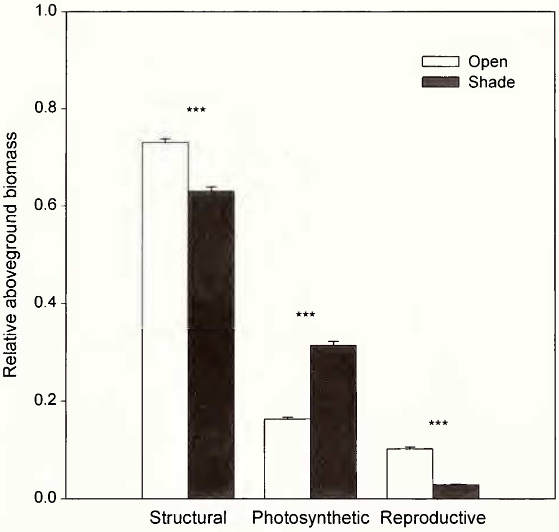

FIG. 3. The mean relative biomass + 1 standard error per shoot in *Euphorbia terracina*, plotted for both open (n = 50) and shade (n = 50) plants. *** Indicates P < 0.001 significant difference between open and shade values.

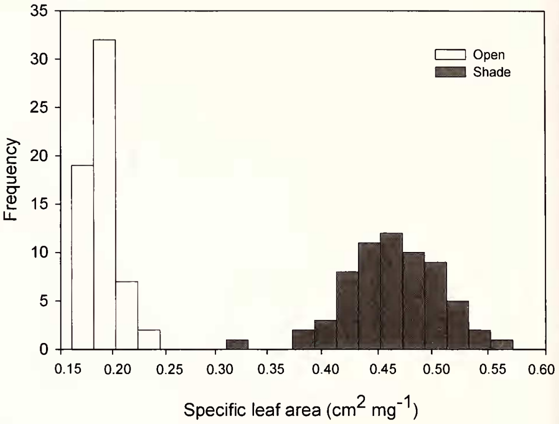

FIG. 4. Histogram of specific leaf area (cm^2 mg^{-1}) of *Euphorbia terracina* for open (n = 60) and shade sites (n = 64).

coastal southern California. Before recent control efforts by NPS, *E. terracina* covered five of the 90 ha in Solstice Canyon, forming dense monocultures in disturbed areas and along the terraces of the riparian corridor, excluding native plants from reoccupying disturbed sites, and thereby altering these costal sage scrub and riparian woodland communities (C. Brigham, personal communication). When compared to a classic study in re-colonization and productivity of *Lotus scoparius*, a native subshrub that forms a significant element of post-fire successional vegetation in California shrublands (Nilsen and Schlesinger 1981), open site *E. terracina* populations in Solstice Canyon had greater total structural, photosynthetic, and reproductive aboveground biomass per square meter (Table 2).

Impacts on species richness and biodiversity of native flora were not surveyed in this study, but field observations suggest that *E. terracina* had a large negative impact once established in the area, strongly altering the natural plant community composition. Although competition was not addressed in this study, biomass can be predictive of competitive ability (Gaudet and Keddy 1988). A greater biomass of *E. terracina* compared to *L. scoparius* may indicate an ability to establish and propagate well in competition with native species, however, biomass data from additional species and manipulative experiments are necessary to evaluate this hypothesis.

Phenotypic plasticity, as illustrated by the considerable difference in phenology, biomass allocation, and leaf morphology between open and shade plants, may explain the success of *E. terracina* in two strikingly different habitats. Field observations established that open site plants began flowering and fruiting 3-weeks earlier in the season, illustrating plasticity in phenology that may have contributed to the difference in relative reproductive biomass allocation. Greater relative biomass allocation to photosynthetic structures and higher specific leaf area in shade plants likely reflect a growth strategy for light capture in a low light environment (Baruch et al. 2000; Monaco et al. 2005). In contrast, low SLA, as evident in the open site plants, has been correlated with a longer leaf life span, lower photosynthetic rates, low soil moisture availability, and high light environments, and thus stress tolerance (Givnish 1988; Reich et al. 1992; Reich et al. 1999). This suggests *E. terracina* is able to respond to both the low light of the riparian woodland corridor and the water stress and higher light intensity characteristic of a sunny coastal slope. As this study is limited to one sun and shade site, further investigation is needed to determine to what extent phenotypic plasticity in response to light may account for the observed differences in populations. Nonetheless, phenotypic plasticity in response to environmental conditions has been proposed to explain an exotic species' successful invasion into a broad range of habitats (Baker 1974; Schweitzer and Larson 1999; Daehler 2003; Parker et al. 2003). *Euphorbia terracina* represents a substantial threat to a range of habitats in coastal southern California.

High SLA compared to native species has also been associated with invasive species (Baruch and Goldstein 1999; Smith and Knapp 2001; Durand and Goldstein 2001; Grotkopp et al. 2002; Lake and Leishman 2004). Specific leaf area can be thought of as the investment per unit of light-capture surface deployed, and is a critical trait in

TABLE 1. *EUPHORBIA TERRACINA* SPECIFIC LEAF AREA OF OPEN AND SHADE PLANTS. Values are reported as mean ±1 standard deviation, n = 60 for open, n = 64 for shade.

Leaf type	Area (cm^2)	Weight (mg)	Specific leaf area (cm^2 mg^{-1})
Open	1.1±0.34	6.0±1.7	0.192±0.014
Shade	5.3±1.50	11.2±3.26	0.464±0.046

the carbon fixation strategy of plants. Species with a high specific leaf area have a shorter investment return rate and greater potential for fast growth. The specific leaf area of sun populations of *E. terracina* (0.192 cm^2 mg^{-1}) is relatively high in comparison to coastal sage scrub species such as *Salvia mellifera* (0.106 cm^2 mg^{-1}) *Eriogonum cinereum* (0.069 cm^2 mg^{-1}), *Mirabilis californica* (0.114 cm^2 mg^{-1}), and *Encelia californica* (0.181 cm^2 g^{-1} mg^{-1}) (R. Sharifi [UCLA], unpublished data). In addition to leaf traits, the relatively low canopy height and herbaceous growth form of *E. terracina* are traits associated with a short juvenile phase, which is characteristic of invaders in disturbed sites (Rejmanek 1996; Lake and Leisham 2004).

Euphorbia terracina also displays a number of reproductive traits typical of invasive weeds. High reproductive output and small seed mass are associated with rapid colonization and are especially indicative of invaders in physically disturbed, open sites (Rejmanek and Richardson 1996; Reichard and Hamilton 1997; Lake and Leishman 2004). *Euphorbia terracina* is capable of producing over 200 seeds per shoot (C. Brigham, personal observation). The relative allocation of biomass to reproductive tissues is approximate 10%, a value quite close to that reported for *Lotus scoparius*, an effective native colonizer of burned chaparral slopes (Nilsen and Schlesinger 1981). While *E. terracina* does not spread through vegetative reproduction, it is capable of rapid resprouting and growth in response to cutting, another trait that is associated with invasives (Baker 1974).

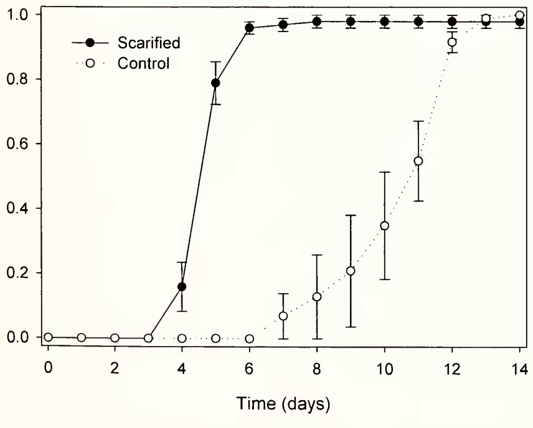

FIG. 5. Mean germination rate (%) plot for lab low light (2 μmol m^{-2} s^{-1}) scarification and control treatments. The mean percent is plotted ±1 standard error for each day (n = 5).

Soil movement by vehicles and earth moving equipment has probably played a significant role in *E. terracina's* spread because of its ability to colonize disturbed sites. Informal observations (P. Rundel, personal observation) suggest that the infestation of seeds into potted plants at local nurseries may be responsible for spread to private property in Los Angeles County. Ant dispersal may also be a factor in the local spread of *E. terracina*, but was not addressed in this study. Many *Euphorbia* species, including *E. terracina*, have seeds with elaiosomes that are ant dispersed (Espadaler and Gomez 1994; Espadaler and Gomez 1996). While this trait is not usually associated with invasiveness (Lake and Leishman 2004), the closely related *E. esula* is ant dispersed in its introduced range (Pemberton 1988).

Euphorbia terracina seeds also display a germination pattern typical of many weedy species. Seeds requiring little or no pre-germination treatment can also be indicative of invasive species (Reichard and Hamilton 1997). The high rates of germination in both control and scarified treatments suggest that *E. terracina* has no deep seed dormancy. Even though scarification was not necessary for germination to occur, it influenced the germination rate, scarified seeds germinated faster than control seeds. The slight lag in germination of control seeds is probably the result of the physical resistance of the seed coat and not related to seed dormancy. *Euphorbia terracina* may also have a substantial soil seed bank, as field observations suggest seed life in the soil is as long as 5–8 yrs or more (C. Brigham, personal communication).

With its high number of invasive traits and successful introduction into various habitats, *E. terracina* poses substantial threat to the native flora of southern California. Phentoypic plasticity in biomass allocation and SLA suggest *E. terracina* could be capable of invading a range of habitats in southern California. Its high SLA compared to native species, herbaceous growth form, reproductive output, rapid regeneration, and success in disturbed sites are all characteristic of weedy, invasive species. Further studies are needed to determine the extent of the impact *E. terracina* has on the native flora and should address its competitive ability for resource

TABLE 2. ABOVEGROUND BIOMASS OF *EUPHORBIA TERRACINA* COMPARED TO *LOTUS SCOPARIUS*. Biomass for each species is measured as mean g m^{-2} and *L. scoparius* data is compiled from Nilsen and Schlesinger (1981). Percent of total biomass is shown in parentheses.

Species	Structural	Photosynthetic	Reproductive	Total
Lotus scoparius	105.6 (64.2)	42.1 (25.6)	16.7 (10.2)	164.4
E. terracina (open)	239.8 (73.9)	51.8 (16.0)	32.7 (10.1)	324.3
E. terracina (shade)	76.0 (64.0)	39.1 (32.9)	3.7 (3.1)	118.8

acquisition compared to native species. The recent and rapid expansion of *E. terracina* suggests that control may not be possible without immediate attention by management agencies. The ability of *E. terracina* to thrive under high disturbance conditions, however, makes it particularly difficult to eradicate as many control treatments, such as mechanical removal and mowing, create conditions that favor further establishment. For *E. terracina*, suppression of the seed germination from the soil seed bank or mulching could be potential control methods, but their success is unknown. Effective management needs to incorporate information gained from ecological studies and must address *E. terracina's* ability to readily germinate and thrive under high light conditions.

Coastal southern California's combination of unique native vegetation, high anthropogenic disturbance, and high number of successful non-native invasions makes invasive species management a high priority. The establishment of invasives in areas of high disturbance has inhibited restoration efforts of native plant communities (Eliason and Allen 1997). Furthermore, urbanization in the Santa Monica Mountains is expected to increase dramatically in the next 25 yrs (Swenson and Franklin 2000), potentially increasing both non-native plant invasions into coastal scrub habitats and the need for ecological restoration in areas disturbed by development. It is therefore important to develop control methods for invasive species. The successful treatment of currrent *E. terracina* populations may prove significant in managing other invasive plant species in the area and protecting already threatened habitats.

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